Multimodality in the individual size distributions of bird communities

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ABSTRACT

Aim Body size often plays a significant role in community assembly through its impacts on the life history and ecological attributes of species. Insight into the importance of size in structuring communities can be gained by examining the distribution of sizes of individuals [i.e. the individual size distribution (ISD) or size spectrum] in a community. ISDs have been studied extensively in aquatic and tree communities, but have received little attention in terrestrial animal communities. Here, we conduct the first macroecological analysis of ISDs in terrestrial animal communities to determine whether they show broad-scale consistency in shape.

Location North America, north of Mexico.

Methods Using likelihood-based methods and Gaussian mixture modelling, coupled with data from the Breeding Bird Survey and Christmas Bird Count, we determine whether the ISDs for thousands of breeding and wintering North American bird communities are: (1) monotonically decreasing, (2) unimodal or (3) multimodal.

Results We find that avian ISDs are consistently multimodal, with most characterized by more than five modes in both breeding and wintering communities from local to continental scales. In addition, the positions of these modes along the size axis are remarkably consistent.

Main conclusions The striking consistency in the ISD within bird communities, as with tree and aquatic communities, indicates that the ISD is an important and informative characterization of resource utilization within an ecological assemblage. The differences in shape of the ISD among these groups also suggest that differences in body size-related constraints affect interactions within a group and with the environment. Our results confirm that avian assemblages do exhibit structure along the body size axis, and therefore it will be fruitful to explore this pattern in greater detail.

Keywords

Birds, community assembly, community structure, multimodality, North America, size distributions, size spectra.

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INTRODUCTION

The role of body size in community assembly has constituted a major thrust of ecological research ever since Hutchinson & MacArthur (1959) proposed that mass-related differences among species could influence niche partitioning and create predictable community patterns (e.g. Gaston & Blackburn, 2000). While Hutchinson & MacArthur (1959) focused on the species size distribution (SSD) – the frequency distribution of species-level average masses – this distribution does not include information on abundances of the component species. The individual size distribution (ISD) – the frequency distribution of sizes of individuals within an assemblage – incorporates abundance and thereby provides insight into how resources are partitioned among size classes irrespective of species identities (White *et al.*, 2007).

ISDs have been studied extensively in both aquatic systems (e.g. Sheldon & Parsons, 1967; Kerr & Dickie, 2001; Stead *et al.*, 2005) and tree communities (e.g. Enquist & Niklas, 2001; Muller-Landau *et al.*, 2006; Coomes & Allen, 2007), revealing both generalities and differences in observed forms of ISDs. Overall, these communities consistently exhibit monotonically decreasing distributions, reflecting constraints of life history and growth (e.g. Enquist & Niklas, 2001; Kerr & Dickie, 2001; Muller-Landau *et al.*, 2006). However, aquatic ISDs, often referred to as size spectra, are also characterized by secondary internal modes reflecting the strong body size–trophic level structuring in those communities (Kerr & Dickie, 2001). Insights gained from these systems have shown that the macroecological study of ISDs is a powerful approach for studying the community-level implications of body size (e.g. Roy *et al.*, 2000; Enquist & Niklas, 2001; Kerr & Dickie, 2001; Andersen & Beyer, 2006; Muller-Landau *et al.*, 2006).

Other than for tree communities, relatively few ISDs have been characterized in terrestrial systems (Cyr *et al.*, 1997; Kerr & Dickie, 2001; White *et al.*, 2007), but these few have revealed substantial variability in structure. Three major forms have been documented: (1) monotonically decreasing, typically described by power functions (Morse *et al.*, 1985); (2) unimodal, approximately described by symmetric or right-skewed lognormal distributions (Schoener & Janzen, 1968; Siemann *et al.*, 1996; McClain & Nekola, 2008); and (3) multimodal, where the distribution is characterized by multiple peaks (Griffiths, 1986; Ernest, 2005). Comparison and interpretation of these shapes are confounded by the diversity of approaches used to characterize them, many of which (e.g. histograms and kernel density estimation) are sensitive to choices of bin width and bandwidth, respectively (Silverman, 1986). Also, these few studies encompass a wide range of taxa (e.g. mammals, insects, gastropods) and temporal and spatial scales. As a result, it is unclear whether differences in ISDs result from statistical, taxonomic, spatial scaling or environmental differences, or whether ISDs in terrestrial animal communities are inherently more idiosyncratic than in tree and aquatic communities. Extensive study of the ISD for a terrestrial animal group across a broad spatial extent using a standardized approach is therefore needed to resolve these issues.

Here, we conduct the first continental-scale macroecological analysis of ISDs in terrestrial bird communities to determine whether the ISD for a group of terrestrial animals shows broad-scale consistency in shape, as seen in tree and aquatic communities. We show that broad-scale consistency does exist for bird communities, and we discuss several hypotheses for size-structured communities that are consistent with this observation. We also address previous statistical issues for evaluating modality (e.g. Manly, 1996; Siemann & Brown, 1999) by using Gaussian mixture modelling (GMM), a well-established statistical method designed explicitly for this purpose (Pearson, 1894; McLachlan & Peel, 2000, and references therein), and maximum likelihood estimation to determine the best-supported number of components in the distributions (McLachlan & Peel, 2000).

METHODS

Data

We used species abundance data from the Breeding Bird Survey (BBS; Sauer *et al.*, 2007) and Christmas Bird Count (CBC; National Audubon Society, 2002) and species body mass data from Dunning (2008). The CBC and BBS are standardized sampling efforts that occur annually, typically in December and June, respectively, at thousands of sites throughout North America. The BBS sampling protocol includes 50 3 minute point counts conducted by one observer every 800 m along a 40-km route. The CBC protocol involves multiple observers censusing a 24.1 km (15 mile) diameter count circle over an entire day. We used data from locations in the United States and Canada that had been sampled in each of the five most recent years of available data (BBS, 2003–07; CBC, 2002–06), yielding 1724 CBC sites and 1829 BBS sites. Data were restricted to diurnal land birds, both native and exotic, including 410 species in the CBC data and 379 species in the BBS data. Due to differences in sampling effort, site-level abundances (summed over the 5-year analysis period) often differed by orders of magnitude between the datasets, with CBC site abundances averaging 127,450 (total number of individual records = 219,724,223) and BBS route abundances averaging 3404 (total = 6,225,789).

Estimating individual-level body size

Because the CBC and BBS do not include individual size measurements, it is necessary to estimate individual-level size distributions. While ISDs could be calculated by assigning a mean species-level mass to every individual of that species, doing so eliminates realistic intra-specific variation. We used mean and variance data for North American bird species from Dunning (2008) to construct more realistic ISDs. Because variance data in Dunning (2008) were not available for all species, we used available data on means and standard deviations of mass (Dunning, 2008; $n = 376$) to construct a scaling relationship between the mean and the variance of body mass (m): $\mathrm{var}(m) = 0.0055\bar{m}^{1.98}$ ($R^2 = 0.92$; Fig. 1a). The strong relationship between mean and variance allows us to estimate the continuous ISD by randomly sampling the individual sizes for each species from a normal distribution with the mean mass from Dunning (2008) and the variance estimated from the above equation. While this approximation introduces a potential source of error, the use of this scaling relationship represents a significant advance that enables these large-scale datasets to be used for a new array of previously intractable questions. Masses from Dunning (2008) were averaged across sexes and subspecies to generate mean masses for each species. We used eBird's hierarchical taxonomy (eBird, 2009) and foraging guild designations (including granivore, frugivore, nectarivore, omnivore, insectivore, insectivore/omnivore and herbivore) from Ehrlich *et al.* (1988).
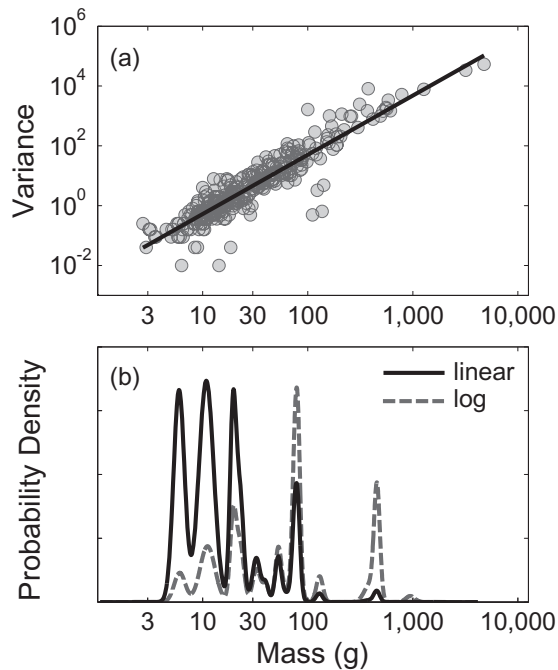
Figure 1 (a) The relationship between the mean (m) and the variance of mass (var(m)) of North American diurnal landbirds (data from Dunning, 2008), used in the estimation of individual sizes for all analyses. The black line represents the power law describing the relationship $\mathrm{var}(m) = 0.0055\bar{m}^{1.98}$ based on the linear regression of $\log(\mathrm{var}(m))$ on $\log(\bar{m})$. (b) Example of the individual size distribution for a Christmas Bird Count site, displayed as both a probability density function (PDF) of log(mass) (log; dashed grey line) and as a PDF of untransformed mass based on converting the logarithmically based PDF to the linear equivalent (linear; black line). Because the PDF of untransformed mass is presented on a logarithmic scale, the heights of the PDFs are not easily compared, and we have used different axes to facilitate visualization. The y-axis for the PDF of mass ranges up to 0.15, while the y-axis of the PDF of log(mass) reaches 5. Logarithmically based estimates exhibit greater densities at larger sizes when compared with the linear estimate.

Characterizing the individual size distribution

Using individual-level masses, we fitted the three major classes of frequency distributions to the data. We used the power law to characterize the monotonic decrease. Specifically, we fitted the truncated Pareto distribution to $\log_{10}$-transformed data using mle_truncpareto.m from White *et al.* (2008), estimating the true minimum and maximum sizes using observed values (which overestimates the quality of the fit and is therefore conservative in this context). This produces an estimate of the frequency distribution of sizes comparable to traditional analyses of ISDs in trees (e.g. Enquist & Niklas, 2001; Muller-Landau *et al.*, 2006) and the number density spectrum used in aquatic systems (*sensu* Andersen & Beyer, 2006), with the data transformation affecting the exponent (but not the form) of the power function (White *et al.*, 2008). We fitted unimodal and multimodal distributions using Gaussian mixture modelling (GMM) on $\log_{10}$-transformed masses.

We performed all analyses in MATLAB (R2009a, The Mathworks, Inc.) using the gmdistribution.fit function for GMM, which implements the expectation-maximization (EM) algorithm for maximum-likelihood estimation (McLachlan & Peel, 2000). We evaluated the fit of 1 to 15 Gaussians for each logarithmically transformed ISD. We compared fits of all distributions (including the truncated Pareto) using Akaike's information criterion (AIC) and the Bayesian information criterion (BIC), using a conservative minimum Δ_i of 10 to designate a specific fit as unsupported (Burnham & Anderson, 2002). The AIC is known to overestimate the number of distributions in mixture models, whereas the BIC underestimates it (Henson *et al.*, 2007; Dornelas & Connolly, 2008). We present only the results of model selection using AIC, as the general conclusions are unaffected by the choice of information criterion. The output of each GMM was a probability density function (PDF) comprising the best-supported number of components evaluated at regular intervals (0.001 $\log_{10}$ units) along the logarithmically transformed body size axis. The number of modes and their positions for the best fitting PDF were determined using the extrema function from the Mathworks File Exchange (Aguilera, 2007), because the PDF can have fewer modes than component distributions.

Computing power and increased convergence failures (a limitation of EM; McLachlan & Peel, 2000) limited our ability to directly analyse ISDs at the larger spatial scales, as well as for local sites with more than a million individuals ($n = 24$ CBC sites). To overcome these limitations, we subsetted the data for each high n site, Bird Conservation Region, biome and the continent (see Influence of spatial scale below) to approximately 1 million individuals while maintaining the observed species abundance distribution for each individual region. We did this by multiplying the relative abundance of each species by 1 million and rounding this number to the nearest integer, with each species having a minimum of one individual.

Use of the logarithm of mass

Absolute size differences have decreasing relative importance for biologically meaningful attributes with increasing size (i.e. the difference between a 10 g and a 20 g bird is much greater than the difference between a 1000 g and a 1010 g bird; Gingerich, 2000; Kerkhoff & Enquist, 2009). Therefore, for questions related to community structure, the frequency distribution of log-transformed sizes is the quantity of interest. This is why SSDs in animal communities are typically constructed using logarithmic binning (e.g. Hutchinson & MacArthur, 1959; Brown & Nicoletto, 1991), why observed unimodal ISDs are on the logarithmic scale (e.g. Schoener & Janzen, 1968; Siemann *et al.*, 1996) and why some models of the ISD explicitly yield predictions for the distribution of the logarithm of mass (e.g. Reuman *et al.*, 2008). The PDFs of log(mass) presented here are equivalent to the distribution of untransformed (or normalized) biomass among size classes, and thus the biomass spectrum typically studied in aquatic communities (e.g. Kerr & Dickie, 2001; Andersen & Beyer, 2006). However, studies of ISDs

in tree communities typically use linear bin sizes (e.g. Enquist & Niklas, 2001; Muller-Landau *et al.*, 2006; Coomes & Allen, 2007). For comparison with tree studies, we converted our GMM fits (which are descriptions of the frequency distribution of log(mass)) back to the linear scale to describe the frequency distribution of untransformed mass, using standard methods (e.g. Buch-Larsen *et al.*, 2005; Andersen & Beyer, 2006; Stegen & White, 2008). This is equivalent to normalizing the number of individuals in a bin by the linear width of the bin as is typically done in the aquatic size spectrum literature (e.g. Kerr & Dickie, 2001). The resulting differences in shape between the distributions of log(mass) and mass are exemplified in Fig. 1(b). The distribution of untransformed mass exhibits the decreasing trend in abundance with size that typifies most communities and consequently de-emphasizes the modes at large sizes relative to the distribution of log(mass). However, the number of modes in each distribution is similar and strongly correlated (BBS, $y = 0.997x$, $R^2 = 0.85$, $P < 0.001$; CBC, $y = 0.992x$, $R^2 = 0.91$, $P < 0.001$), and so we present only results from the original GMM PDFs.

Consistency in mode position among sites

Potential consistencies in mode positions across sites were evaluated by pooling all mode positions identified for each site-level PDF for each dataset. We then generated kernel density estimates (KDE) of the distributions of mode positions, using the data-driven solve-the-equation plug-in method for optimal selection of the bandwidth (h) for the KDEs (Sheather & Jones, 1991), as implemented by Raykar & Duraiswami (2008). We determined the optimal value of h for each dataset (BBS, $h = 0.0155$; CBC, $h = 0.0108$) and then used the average (0.0132) to generate the KDEs for more meaningful comparison. If the mode position varies widely across sites, then these KDEs will have broadly defined modes, whereas if the mode position is highly conserved, then at those body sizes the KDE will exhibit narrowly defined peaks.

Influence of spatial scale

To assess if and how the shape of ISDs changes across spatial scales, we aggregated ISDs from local sites (i.e. BBS routes and CBC circles) into successively larger groups prior to analysis. We used 37 North American Bird Conservation Initiative Bird Conservation Regions (BCRs), defined by similarities in bird communities and the environment (Sauer *et al.*, 2003), to aggregate the site-level data. Geographic boundaries for each BCR were obtained online (http://www.bsc-eoc.org/international/bcrmain.html; accessed 24 January 2009). Based on Reichenbacher *et al.*'s (1998) biome classifications, we also aggregated sites into 10 geographically coarser biomes (see Table S1 and Fig. S1 in Supporting Information). For the continental analysis, individuals from only a subset of sites were aggregated to control for disparities in regional sampling intensity. For each dataset, we selected 10 sites from each cell of a 5 decimal degree square grid covering North America to include in the aggregate analysis (or fewer, if data were not available for 10 sites).

RESULTS

Individual size distributions of both breeding and wintering avian assemblages were consistently multimodal from local to continental scales (Figs 2–4, S1 & S2). Numbers of modes identified in ISDs of local communities ranged from 2 to 14 for the BBS (median = 9) and from 1 to 13 for the CBC (median = 9; Fig. 3). Median number of modes in ISDs did not change markedly with increasing spatial scale, with even continental-scale distributions exhibiting significant multimodality (BBS, 8; CBC, 9; Figs 3 & 4). We found no support for either a monotonically declining or a unimodal form in ISDs at any spatial scale (all ΔAIC > 100), except for three CBC sites (out of 1724 sites). These sites all had unimodal ISDs and either contained only one species ($n = 1$) or were overwhelmingly dominated by red-winged blackbirds (*Agelaius phoeniceus*; $n = 2$). Examples of ISDs from local communities are depicted in Fig. 2, with both PDFs generated by GMM and properly scaled histograms of $\log_{10}(\text{mass})$ presented for comparison. Relationships between the number of modes in a site's ISD and the number of individuals, species and trophic guilds censused at the site were weak for both datasets (all $R^2 < 0.01$, except for individuals versus modes for CBC sites, $R^2 = 0.07$).

Similarities in the general form of the ISDs of breeding and wintering birds result despite differences in species composition, population densities (median local density, BBS = 122.7 individuals km^{-2}; CBC = 73 individuals km^{-2}), and sampling area of the datasets (BBS route ≈ 25 km^2; CBC circle ≈ 458 km^2). However, the shapes of the distributions, i.e. the areas under the curve of each mode, clearly differ between datasets (Figs 2, 4, S1 & S2). This is exemplified by the continental ISDs, which demonstrate the compositional differences between breeding and wintering bird assemblages (Fig. 4). Breeding birds are more equitably distributed along the body size axis, reflecting the seasonal departure of smaller migratory species and the greater degrees of dominance by individual species in specific size classes in winter communities (e.g. the most dominant bird in both assemblages is the red-winged blackbird, but it only comprises *c.* 10% of terrestrial breeding birds relative to *c.* 40% of wintering birds).

The number of species and trophic guilds represented within each mode also behaved similarly across the seasonal assemblages and across spatial scales (Fig. S3). For all but the continental scale, the frequency distribution of number of species per mode is positively skewed, with many modes containing only one species and a decreasing number of modes containing increasing numbers of species (Fig. S3). However, only a small fraction of modes actually contained a single species (CBC, 9.8%; BBS, 12.1%) or a single trophic guild (CBC, 18.1%; BBS, 17.6%). Frequency distributions of the number of trophic guilds are, on the other hand, generally unimodal, with about half of the modes including representatives from three out of seven trophic guilds in the local assemblages of both breeding and
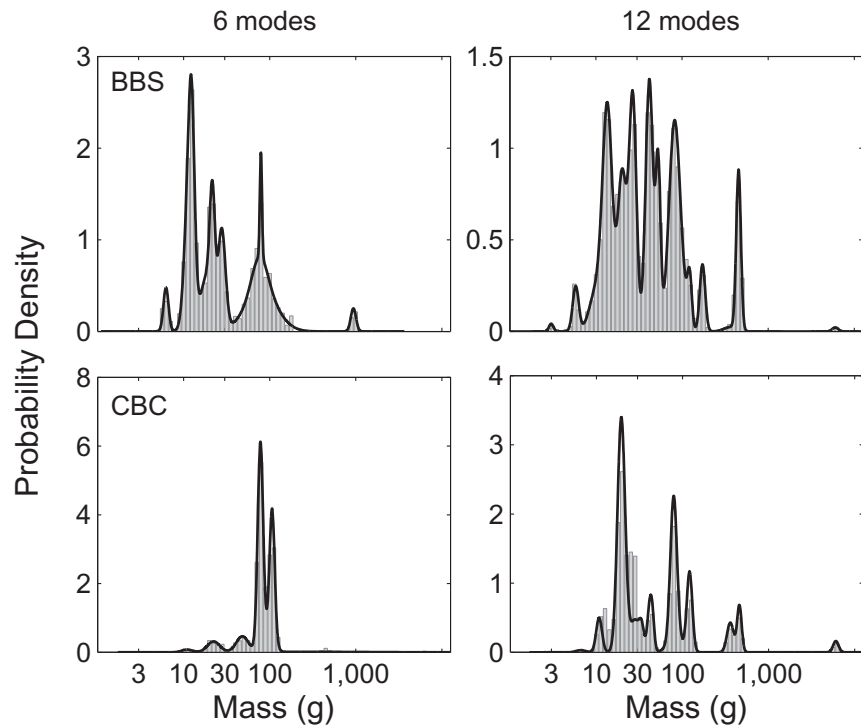
Figure 2 Examples of individual size distributions from four sites spanning both datasets (BBS, Breeding Bird Survey; CBC, Christmas Bird Count). Grey bars represent scaled histograms of logarithmically binned individual sizes. Bin widths for histograms were based on output of the Gaussian mixture modelling (GMM) and are approximately 0.05. The black lines represent the probability density functions generated via GMM.

wintering birds. Assemblages at larger spatial scales tend to have more modes that include representatives from four or five trophic guilds, with ISDs of CBC assemblages tending to include more guilds in body size modes than those of BBS assemblages (Fig. S3).

Finally, the consistency in the locations of the modes in the ISDs along the body size axis within and between the two datasets is striking. The within-dataset, across-site consistency is indicated by the spiky nature of the KDEs of mode locations, i.e. the very narrow and dramatic peaks in the distributions (Fig. 5). This is indicative of little variability in the positions of modes. For example, the ISDs of 27% of CBC sites and 23% of BBS sites include the 'starling mode', if delineated using the peak (*c*. 78 g) and local minima depicted in Fig. 5, and 27% of CBC and 24% of BBS site-level ISDs contain the 'chickadee mode' (*c*. 12 g). The similarity between the datasets is readily apparent, and quantification yields a 77% overlap between the two KDEs. All 15 distinct mode positions are shared between the assemblages, although the mode around 3 g, populated by the hummingbirds (Trochilidae), is poorly represented in winter assemblages. Note that since the number of modes in site-level ISDs is quite variable (Fig. 3), not all sites contain modes at all positions depicted in Fig. 5. This figure also demonstrates that not all positions along the body size axis yield modes in local ISDs.

DISCUSSION

Individual size distributions of avian assemblages in North America are clearly and consistently multimodal. This pattern holds for both breeding and wintering assemblages and across all spatial scales, from local communities to regional and conti-

nental pools (Fig. 3). This form of the ISD deviates strongly from the two most commonly described forms of the ISD: (1) the monotonic decline exhibited in aquatic communities (e.g. Kerr & Dickie, 2001; Andersen & Beyer, 2006) and insect (e.g. Morse *et al.*, 1985) and tree assemblages (e.g. Enquist & Niklas, 2001; Muller-Landau *et al.*, 2006); and (2) the log-unimodal form of the ISD that describes some insect (Schoener & Janzen, 1968; Siemann *et al.*, 1996) and deep-sea gastropod (McClain, 2004) communities. Moreover, the vast majority of ISDs contain more than five modes, with similar ranges and median numbers of modes exhibited by breeding and wintering assemblages (Fig. 3). The consistency of this result across thousands of bird communities, in combination with smaller studies of both birds (Griffiths, 1986) and mammals (Ernest, 2005), strongly suggests that multimodality is a general property of terrestrial vertebrate assemblages.

Multimodality in aquatic size spectra (e.g. Sheldon & Parsons, 1967; Sheldon *et al.*, 1972; Cyr & Pace, 1993; Stead *et al.*, 2005) typically results from the inclusion of multiple trophic/ functional groups (e.g. bacteria, phytoplankton, zooplankton), with each trophic group corresponding to a mode (Kerr & Dickie, 2001 and references therein; McClain & Nekola, 2008). This observation has facilitated modelling of size distributions based on predator–prey size ratios and trophic efficiencies (Kerr & Dickie, 2001). In contrast to this one-group–one-mode pattern, we find that bird assemblages typically have more than one trophic group in each mode (>80% of modes have two or more groups), even at local spatial scales (Figs 5 and S3; notable exceptions include a hummingbird mode near 3 g and a turkey mode near 6000 g). These differences probably occur because the ecology of terrestrial animal groups is not as strictly gov-
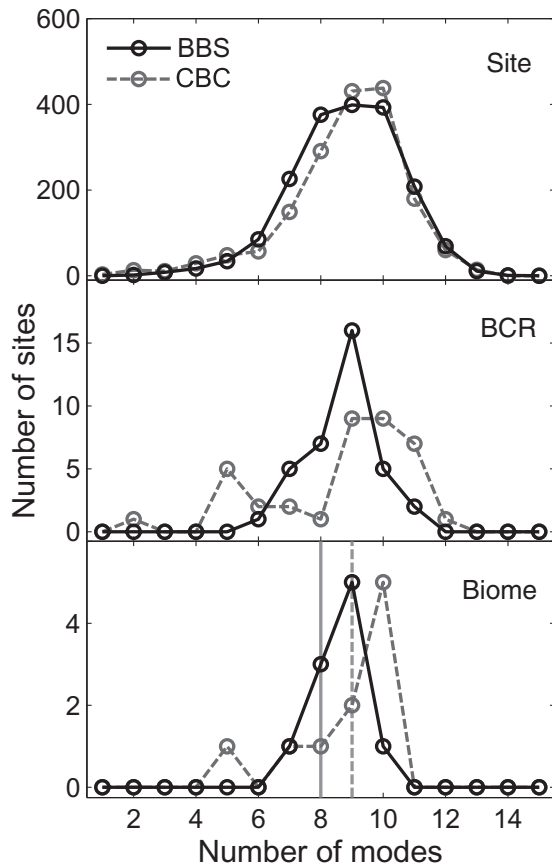
Figure 3 The number of modes identified in individual size distributions (ISDs) across spatial scales and datasets. The number of modes identified in the continental-scale ISDs are indicated by the vertical lines in the bottom panel. Multimodality in the ISD is ubiquitous in North American bird assemblages. BBS, Breeding Bird Survey (black lines); CBC, Christmas Bird Count (dashed grey lines); BCR, Bird Conservation Region.

erned by size as in aquatic systems, and therefore the processes underlying multimodality in these systems are probably distinct.

Perhaps the most famous model predicting multimodality in terrestrial size distributions is Holling's (1992) textural discontinuity hypothesis (TDH). According to the TDH, ecological and environmental processes operating at multiple spatial and temporal scales result in scale-dependent resource availability, with specific scales more accessible to organisms of particular sizes. This results in resources being irregularly available along the body size axis, and, in turn, clusters of species at sizes that can access those resources, thus driving multimodality in size distributions (Holling, 1992; reviewed in Allen *et al.*, 2006). Therefore, this hypothesis, and consequently any test of it, assumes that resource use is a reflection of resource availability, which although likely in most, may not hold in all systems. Interestingly, the TDH has almost never been evaluated using individual-level data (but see Ernest, 2005), but rather is typically assessed by looking for multimodality in the species size distribution. While substantial evidence for multimodality in SSDs has been presented for terrestrial assemblages (e.g.
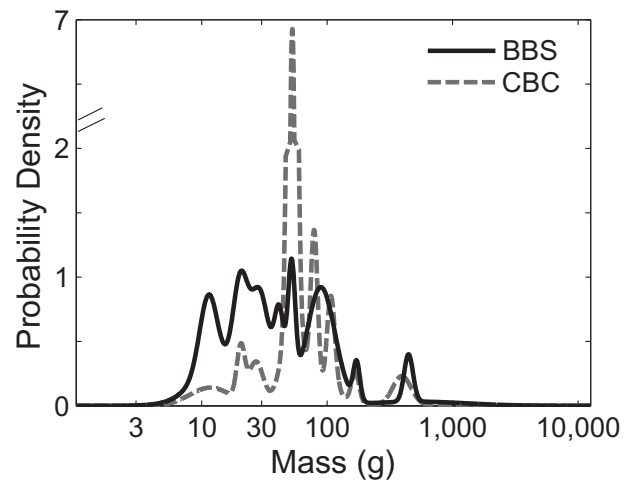

Figure 4 Continental-scale individual size distributions of the Breeding Bird Survey (BBS, black line) and Christmas Bird Count (CBC, dashed grey line). Probability density functions were generated using Gaussian mixture modelling on a subsample of sites selected to maintain geographically consistent sampling intensity (see text for details). Note the split *y*-axis.

Holling, 1992; Allen *et al.* 2006, and references therein; Skillen & Maurer, 2008; Kelt & Meyer, 2009), this is a less direct test of the TDH than evaluating multimodality in currencies more directly related to resource use, such as abundance (or estimates of energy use; see Ernest, 2005).

Our results, based on large sample sizes in combination with the use of well-established statistical methodology, clearly support the central prediction of the TDH: resource use, as approximated here by abundance, is strongly clustered with respect to body size. In some cases this clustering appears to represent actual discontinuities along the size axis, while in others there is simply a decline in the probability of occurrence (e.g. Fig. 2). Since it is technically not feasible to distinguish between low-probability events and discontinuities (i.e. events with probability zero), we refer to this structure simply as multimodality. Further analysis of the relationship between habitat structure and the detailed form of ISD multimodality should provide further insight into the importance of textural discontinuity for structuring ecological systems.

An alternative model for multimodality, here called the self-organization hypothesis (SOH), was recently proposed by Scheffer and van Nes (2006). In this hypothesis, multimodality results because individuals of species sufficiently similar in size coexist through neutral processes and compose a single mode, whereas individuals sufficiently different in size coexist through character displacement, generating a series of modes separated by sufficient distance to allow coexistence. In the SOH, multimodality is generated through species interactions rather than underlying resource architecture as in the TDH. Because community assembly in the SOH is dependent on stochastic assembly, the location of modes in the simplest SOH models is idiosyncratic from community to community. Our results do not support this prediction of idiosyncrasy in mode location.

Figure 5 Kernel density estimates of the mode positions of all site-level individual size distributions from each of the two datasets (BBS, Breeding Bird Survey; CBC, Christmas Bird Count), using an optimal $h = 0.0132$ (see text for details). Silhouettes represent common species or species groups that contribute to the corresponding mode location, from left to right: hummingbird, kinglet, chickadee, sparrow, red-winged blackbird, starling, mourning dove, quail, rock dove, raven, turkey. (Artist credit: Suellen Jacob.)
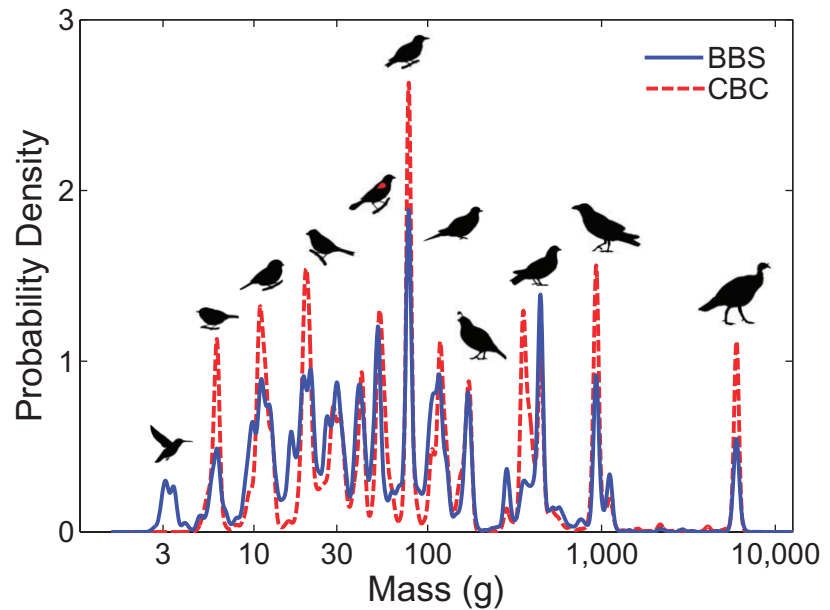
Instead, we found that avian assemblages exhibited regular positioning of the modes across communities, despite major differences in ecosystem type and species composition (Fig. 5). The consistency in modal position along the body size axis strongly suggests that body size is indeed an important structuring characteristic in these communities and that its influence is regular rather than idiosyncratic. In addition, if the position of modes at the community scale was effectively random, we would expect the random variability in mode position among sites to result in smoother, potentially uniform, distributions as the spatial scale of analysis increases. This is not supported in North American birds, which continue to exhibit multimodality even at continental scales (Figs 3 & 4).

However, Scheffer and van Nes (2006) address two potential mechanisms that might lead to consistency in mode position. They state that the positions of modes will generally be determined by 'coincidental clumps in the . . . initial species distribution' which 'serve as random condensation points'. Therefore, local communities that are assembling from regional pools with the same size structure may have similar distributions as a result of similar starting conditions. In fact the well-identified mode at *c.* 30 g in the avian SSD (Brown, 1995) or the well-defined modes in the continental ISDs (Fig. 4) could serve as anchors that result in similar mode positions in local communities. This would mean that the important structuring processes for avian ISDs operate at continental and/or evolutionary scales and that local distributions do not actually reflect local conditions. Alternatively, Scheffer and van Nes (2006) showed that differences in suitability along the niche axis (the size axis in this case) could result in predictable positions of the different modes. If, as predicted by the TDH, important environmental features result in some sizes being more optimal than others, this could cause consistent positioning of the ISD modes under the SOH model.

The striking consistency in the ISD within three very different ecological groups (trees, aquatic organisms and birds)

indicates that the ISD is an important and informative characterization of resource utilization within an ecological assemblage. That there are consistent differences in ISD shape among these groups is also important, indicating how differences in body size-related constraints will affect interactions within a group and with the environment. While the ISD can provide important insights, body size alone is not expected to fully explain community structure. Many bird species of similar size have very different foraging strategies (e.g. foliage-gleaning, bark-gleaning and ground-gleaning insectivores), and even within a single foraging strategy, the fine-scale partitioning of resources can allow multiple species to coexist (MacArthur, 1958). However, our results confirm that entire avian assemblages do exhibit structure along the body size axis, thus warranting further exploration of this pattern. Differences in life history among taxonomic and trophic groups and shifts in ecological processes along environmental gradients are likely to determine the relative importance of body size in structuring ecological communities. Application of methods such as those presented here to a diverse array of taxa and habitats will ideally lead to a mechanistic understanding of the role of body size in community assembly, as Hutchinson & MacArthur (1959) envisioned.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Probability density estimates of individual size distributions based on Gaussian mixture modelling from all biomes spanning both datasets

Figure S2 Probability density estimates of individual size distributions based on Gaussian mixture modelling from all Bird Conservation Regions spanning both datasets

Figure S3 Frequency distributions of the number of species and guilds that comprise each mode across all sites

Table S1 Biome classification used in this study

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BIOSKETCH

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